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Breaching the dispersal barrier to invasion: quantification and management

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Abstract. Globalization has resulted in unprecedented movements of people, goods, and alien species across the planet. Although the impacts of biological invasions are widely appreciated, a bias exists in research effort to post-dispersal processes because of the difficulties of measuring propagule pressure. The Antarctic provides an ideal model system in which to investigate propagule movements because of the region's isolation and small number of entry routes. Here we investigated the logistics operations of the South African National Antarctic Programme (SANAP) and quantified the initial dispersal of alien species into the region. We found that over 1400 seeds from 99 taxa are transported into the Antarctic each field season in association with SANAP passenger luggage and cargo. The first ever assessment of propagule drop-off indicated that 30–50% of these propagules will enter the recipient environment. Many of the taxa include cosmopolitan weeds and known aliens in the Antarctic, indicating that logistics operations form part of a globally self-perpetuating cycle moving alien species between areas of human disturbance. In addition, propagules of some taxa native to the Antarctic region were also found, suggesting that human movements may be facilitating intra-regional homogenization. Several relatively simple changes in biosecurity policy that could significantly reduce the threat of introduction of nonnative species are suggested.

Key words: Antarctica; biosecurity; Gough Island; intra-regional movement; invasion; invasion pathway; Marion Island; propagule pressure; seed dispersal.

Introduction

Increasing globalization and human movement have amplified the rates and extent of species introductions. Most habitats on the planet now harbor introduced species, and, for many groups, no asymptote to introductions is in sight (McKinney and Lockwood 1999, Sala et al. 2000, Davis 2003, Sax and Gaines 2003, 2008, Meyerson and Mooney 2007). Moreover, once established, some alien species are able to colonize a variety of environments, substantially reducing populations of selected indigenous species (sometimes to extinction; e.g., Blackburn et al. 2004) and/or fundamentally altering ecosystem functioning (Mack et al. 2000, Richardson and van Wilgen 2004, Asner and Vitousek 2005). These impacts can be substantial, both in ecological and economic terms (Pimentel et al. 2000, Marais et al. 2004). In consequence, translocation of species by humans is recognized as one of the most significant threats to global biodiversity (Ricciardi 2007) and has been accorded a high status in policy interventions and research agendas (Millennium Ecosystem Assessment 2005, Buckley 2008, Hulme et al. 2008).

The ecological and economic significance of invasions have been recognized formally at least since Elton's (1958) early work, but in a more comprehensive, directed fashion since the inception of the SCOPE program on biological invasions (Macdonald et al. 1986, Mooney and Drake 1989). Much research effort has now been focused on both understanding and predicting invasions, specifically the traits of species that become invasive and which communities or areas might be most invasible (Daehler 2003, Duncan et al. 2003, Richardson and Pyšek 2006). Although several general patterns have emerged (e.g., Lawton and Brown 1986, Pyšek 1998, Lockwood 1999, Vazquez and Simberloff 2001, Prinzing et al. 2002, Thuiller et al. 2005, Richardson and Pyšek 2006, van Kleunen et al. 2008), perhaps one of the strongest is the significant role of propagule pressure both for introduction and for invasion success (Williamson 1996, D'Antonio et al. 2001, Rouget and Richardson 2003, Lockwood et al. 2005, Memmott et al. 2005). Moreover, from a management perspective, the substantially lower costs of prevention relative to later control have been widely recognized (Mack et al. 2000, Courchamp et al. 2003, Gren 2008). In consequence, the importance of understanding propagule pressure and the pathways of introduction has been repeatedly emphasized (Minton et al. 2005, Wonham et al. 2005, Hulme et al. 2008, Reaser et al. 2008, Sax and Gaines 2008).

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For intentionally introduced species, initial propagule translocation constitutes a single process. However, for unintentionally transported species, which often have small and cryptic propagules, initial propagule translocation should in fact be split into two distinct phases: entrainment, when propagules become associated with a vector and transported from source points to new locations, and drop-off, when those propagules become disassociated from their vector and enter the recipient environment. These are the first steps in a multistep process (translocation, establishment, spread) that might result in eventual invasion of a given area and transformation of local systems (see Elton 1958, Carlquist 1965, Richardson et al. 2000, Williamson 2006, Theoharides and Dukes 2007, Milbau and Stout 2008). The transitions from introduction to establishment and from establishment to invasion are becoming increasingly well investigated (Duncan 1997, Grevstad 1999, Blackburn and Duncan 2001*a*, *b*, Miller et al. 2002, Roy et al. 2002, Wolfe 2002, Cassey et al. 2004, Forsyth et al. 2004, Suarez et al. 2005). By contrast, initial dispersal pathways and particularly propagule deposition are much more poorly studied (Puth and Post 2005). Although some early investigations were concerned with pathways and propagule pressure along them (Wace 1977, Macdonald et al. 1986) and the numbers of such studies are now increasing (e.g., Whinam et al. 2005, Caton et al. 2006, Lewis et al. 2006, Liebhold et al. 2006, Ward et al. 2006, Blackburn and Cassey 2007, Lee and Chown 2007, Davidson et al. 2008), the extent of work remains small. Indeed, in a recent review of plant invasions on islands, Sax and Gaines (2008:11 495) argued that "... propagule pressure of exotic species must be better understood. To date, propagule pressure has been poorly studied in nearly all ecosystems." This lack of information prevents the development of meaningful management plans to mitigate the introduction of alien species (Puth and Post 2005, Hulme et al. 2008). Moreover, it is also true of the Antarctic region, for which only a single study (Whinam et al. 2005) has quantified propagule pressure and pathways.

Here, we address the extent of seed propagule pressure along the major pathways of introduction to the Antarctic region, including the continent and its surrounding islands. This region is suitable for such a study because the isolation of the continent and its islands from other land masses (Clarke et al. 2005) make identification and investigation of the propagule pathways relatively straightforward. What is more, a variety of aliens has successfully colonized the region (reviewed in Frenot et al. 2005; see Plate 1), leading the Antarctic Treaty System responsible for the governance of the area south of 60° S and the nations charged with the management of the islands lying between 40° and 60° S to identify biological invasions as one of the most significant conservation threats in the region, especially given rapid climate change on the sub-Antarctic islands and Antarctic Peninsula (Bergstrom and Chown 1999, Convey 2006, de Villiers et al. 2006, Hull and Bergstrom 2006, Mansfield and Gilbert 2008). Specifically, we quantified the propagule translocation associated with the South African National Antarctic Programme (SANAP) logistics operation. We determined which propagules become entrained with cargo and expeditioner clothing and how this relates to the local source propagule pool, then investigated what proportion of propagules that become entrained drop off and enter the environment. We then examined how this relates to the alien species that are established and consider what insight this might provide into past and present movements of alien species in the region. Finally, we examined how this unintentional transfer can be managed by considering what vector characteristics relate to high propagule load and high propagule drop-off and also the efficacy of commonly employed mitigation measures.

Methods

Study area and background to the SANAP logistics operation

The Antarctic region is typically considered to include the Antarctic continental landmass, the Antarctic Peninsula and its surrounding archipelagos, and a ring of sub-Antarctic islands lying between approximately 40° and 60° S (Smith 1984, Longton 1988, Frenot et al. 2005). Climatic conditions range from the relatively mild temperatures and high rainfall of the sub-Antarctic to the extreme low temperature and dry polar desert conditions in the central Antarctic continent (Convey 1996, Peck et al. 2006). In consequence, the number of established aliens and the potential for future establishment is highest in the sub-Antarctic (Frenot et al. 2005). However, many parts of the region, such as the Antarctic Peninsula, are experiencing rapid climate change, which may facilitate the establishment of alien species in previously unsuitable areas (Frenot et al. 2005). Indeed, several records of new alien species have appeared recently (e.g., Hughes et al. 2005, Lee et al. 2007), and concern has been expressed about the rapid spread of the alien *Poa annua* at a site along the Peninsula (Chwedorzewska 2008).

The South African National Antarctic Programme operates throughout the entire region, using the vessel the *SA Agulhas* to resupply bases on the Islands of Gough (40°20′ S, 09°54′ W) and Marion (46°54′ S, 37°45′ E), as well as the South African National Antarctic Expedition IV base (SANAE, Dronning Maud Land, Antarctica; 71°40′ S, 02°51′ W).

Local propagule pool

Between March 2006 and May 2007 all SANAP cargo was packed at a warehouse in Paarden Eiland, an industrial area close to the main cargo dock in Cape Town. Paarden Eiland has large areas of waste ground supporting substantial stands of weedy species. For the remaining 10 months of this study, the stores were then relocated to a site on the Victoria and Alfred Waterfront (Cape Town), a commercial development with no substantial propagule sources close by.

To establish the taxonomic composition of propagule sources near each of the cargo warehouses, vegetation surveys were undertaken. At each of the two warehouses (Paarden Eiland and Victoria and Alfred Waterfront) all vascular plant species were recorded along four 500 m long transects laid in opposing directions away from each warehouse. Taxonomic composition of the vegetation surrounding the cargo stores was then compared with the taxonomic composition of propagules found in cargo by calculating the proportion of shared taxa.

To determine potential propagule sources for passenger luggage, information on recent travel history was gathered from expeditioners. Passengers were asked to complete an anonymous questionnaire detailing what countries they had visited for more than 24 hours in the previous 12 months. Because of the large area in which propagules could have become entrained in passenger luggage, it was not possible to make a quantitative comparison of propagule pool and entrained propagules. However, data on whether passengers had visited regions that are climatically similar to the areas serviced by SANAP is valuable in elucidating the establishment likelihood of entrained propagules.

Entrainment in cargo

For cargo, propagule surveys were conducted for all resupply voyages during the sampling period. This consisted of two voyages to Gough Island, four voyages to Marion Island, and two voyages to SANAE. The SANAP uses a range of containers to transfer cargo from the central stores in Cape Town to research stations on Marion, Gough, and SANAE. The primary type of container used to resupply Gough and Marion Island is a 4.6 m^3 shipping container, while SANAE is resupplied using mainly 36 m^3 shipping containers. A container, irrespective of size, was considered a single cargo unit.

For each voyage $\sim$20 cargo units were surveyed. To ensure samples were not biased by the way in which cargo units were stored or cleaned prior to use, units were randomly selected from the voyage packing list. Entrained propagules were collected from both the inner and outer surfaces of containers using a vacuum cleaner (Electrolux Ultima 1700 W [Electrolux, Stockholm, Sweden] or Black and Decker V2405 [Black and Decker, Towson, Maryland, USA]) fitted with a nylon mesh filter between the crevice nozzle and the succession pipe and a pair of tweezers. Samples were categorized according to the location of the warehouse, voyage destination, and the volume of the cargo unit.

Entrainment in passenger luggage

Passenger luggage surveys were conducted on 75% of resupply voyages. This consisted of one voyage to Gough Island, three to Marion Island, and two to SANAE. For each voyage $\sim$20 passengers were randomly selected from a passenger list and asked to submit their fieldwork clothing for inspection. Typically this included a pair of waterproof over-trousers, waterproof jacket, polar fleece, woolly hat, gloves, socks, bags, and footwear. Entrained propagules were collected using a similar method to the cargo surveys. For each item of clothing a nylon mesh filter was fitted between the crevice nozzle and the succession pipe of a vacuum cleaner (Philips Performer Animal Care [Philips, Amsterdam, The Netherlands] or Electrolux Ultima 1700 W). Each item then was methodically searched using the crevice nozzle of the vacuum cleaner to collect loose material and a pair of tweezers to pick out deeply entrained material. Whinam et al. (2005) indicated that jacket pockets, the insides of shoes, and seam lines were likely places to find entrained propagules, so particular attention was paid to these areas. Collections were sorted by item and expeditioner. In addition, note was made of whether the item was issued by SANAP (which has all items thoroughly cleaned between field trips) or was the participant's personal property, whether or not Velcro was present on the item, and the destination at which the clothing was to be used.

Identification and statistical analyses of propagules in passenger luggage and cargo samples

Where possible, seeds were identified to genus level using seed identification guides (Botha 1999, Cappers et al. 2006) and online resources (Royal Botanic Gardens, Kew, Seed Information database and Department of Horticulture and Crop Science, Ohio State University Seed ID Workshop; both *available online*).[2,3] In 24 instances for cargo surveys and 33 instances for passenger luggage samples, it was not possible to identify an individual seed to family or genus level. In these instances the seed was assigned to an "unknown morphotype" category.

To determine whether sampling had adequately detected all taxa entrained within both clothing and cargo, rarefaction curves for samples collected on each voyage were constructed at the genus and family levels using the nonparametric Chao 2. This estimator of taxonomic richness uses a function of the number of taxa that occur in one sample (Q) against the number of taxa that occur in two samples (Q_2) (EstimateS version 8.0; Gotelli and Colwell 2001, Magurran 2004). The curve reaches its asymptote at the point at which every taxon has occurred in at least two samples:

$$S_{\mathrm{Chao\ 2}} = S_{\mathrm{obs}} + (Q^2/2Q_2).$$

Taxonomic composition of propagules from cargo and clothing from each of the different categories, as well as overall taxonomic similarity between propagules from cargo and clothing, was compared using one-way

[2] ⟨http://data.kew.org/sid⟩
[3] ⟨http://www.oardc.ohio-state.edu/seedid⟩

analyses of similarity (ANOSIM) based on ranked Bray-Curtis similarities and were conducted in Primer (version 5.1.2, Plymouth Marine Laboratory; Clarke and Warwick 2001). Because of the high number of items that contained very few propagules (see Appendix A for frequency distributions), data were square-root transformed prior to analyses.

The ANOSIM test statistic, R, has a theoretical range between -1 and $+1$ and is a measure of the difference between average ranked values of Bray-Curtis similarities among replicates within (r_w) and between (r_b) treatments:

$$R = (r_b - r_w)/\{[n - (n-1)/2]/2\}.$$

Positive R values represent larger between-treatment compared to within-treatment similarities. An R value of zero represents the null hypothesis of no difference. Negative R values are unlikely as they would correspond to similarities across sites being higher than those within sites. The significance level of the R statistic is calculated by comparing the observed R value to that computed from 1000 random permutations (Clarke and Warwick 2001).

The taxonomic composition of propagules found in clothing and cargo was compared with the taxonomic composition of species known to be established aliens in the Antarctic region as a whole (including all sub-Antarctic islands) by calculating the proportion of shared taxa. In addition, the proportion of shared taxa was calculated individually for Marion and Gough Islands (J. D. Shaw and S. L. Chown, *unpublished data*, based on the database used by Greve et al. [2005]). Comparisons were not made for SANAE as no aliens are known to be established in the Dronning Maud Land region.

Generalized linear models were implemented to compare the numbers of propagules found in the different categories of passenger luggage and cargo. Because the variance of samples exceed the mean (see Appendix A), a log-link function and a negative binomial distribution were used (Proc Genmod, SAS 9.1; SAS Institute, Cary, North Carolina, USA). The number of seeds per item was the response variable. For cargo, packing location and destination were used as categorical predictors and the volume of cargo was included as a covariate. For clothing, item, presence of Velcro, whether or not it was issued by SANAP, and destination were used as categorical predictors.

Propagule drop-off

The proportion of seeds entrained in cargo and passenger luggage that actually enters the environment was experimentally estimated by measuring the degree of propagule drop-off on the resupply voyage to SANAE in December 2007. The annual voyage involves the transport of ~100 expeditioners and 800 m^3 of cargo from Cape Town ~5600 km by ship to the Dronning Maud Land coast. Here cargo is transferred to sledges and towed by tracked vehicle ~150 km inland to the research station. Passengers are flown directly from the vessel to the station by helicopter.

Seeds from three species were used in the propagule drop-off experiment, each representing different size classes of seeds (Liu et al. 2008). The seeds used were: *Avena sativa* (mean mass = 31.5 mg), *Lolium perenne* (mean mass = 2 mg), and *Agrostis stolonifera* (mean mass = 0.06 mg). To ensure homogeneity, seeds were purchased from a bulk seed supply agent (Advance Seed, Krugersdorp, South Africa). Because of strict environmental legislation (see full legislative documentation, *available online*),[4] it was necessary to sterilize all seeds that were to be used in the experiment. To achieve this, seeds were heated to 180°C for 48 h, as pilot trials indicated that this was sufficient to prevent any germination. Seeds were then sprayed with a water-insoluble blue spray paint (Spectra Spray, Johannesburg, South Africa) to ensure ease of re-identification upon recovery. Before deployment, a random sample of the marked, heat-treated seeds was tested to ensure that sterilization was successful by placing groups of 20 seeds on nutrient agar (Merck Biolab bacteriological agar, Wadevile, Gauteng, South Africa) at 21°C with a 12:12 (light : dark) cycle. Seeds were checked daily for evidence of germination.

Partial recovery could inflate the estimate of propagule deposition; therefore, the accuracy of the sampling protocol was estimated prior to conducting this experiment. Thirty seeds (10 from each size class) were placed into each of 10 sets of field clothing, and 300 seeds (100 from each size class) were placed into 20 cargo units that ranged in volume from 4.6 to 36 m^3. The same sampling protocols used for the passenger luggage and cargo surveys were used to recover seeds immediately. Because there was no opportunity for drop-off, if the sampling protocol was 100% efficient, all seeds should be recovered. Therefore, any values lower than 100% can be attributed to sampling inaccuracy. For each seed species on each cargo/luggage type, the number of seeds that were retrieved was counted. This was subtracted from the initial number of seeds, and the result converted to a percentage of the initial number of seeds used per seed type and luggage/cargo type (see Appendix B for data). The experimental values were then corrected using the formula: drop off = initial no. seeds − (recovered number of seeds + [initial no. seeds × mean proportion missed in drop-off trial]).

During cargo packing in Cape Town, 26 cargo units ranging in volume from 4 to 40 m^3 were seeded with 30 seeds/m^3 from each size class. These cargo units were then loaded into the ship's hold and transferred by sleds towed by tracked vehicles to SANAE station. Immediately upon arrival at SANAE station, containers were surveyed using a hand-held vacuum cleaner (Black and

[4] ⟨http://v3.ats.aq/e/cep.htm⟩

TABLE 1. Seeds found in cargo (mean ± SE) sampled at Paarden Eiland and the Waterfront stores on voyages to Gough and Marion islands and to the South African National Antarctic Expedition IV base (SANAE).

Destination, by packing location	No. cargo units sampled	Seed density per unit (no./m^3)
Paarden Eiland		
Gough	22	0.77 ± 0.15
Marion	66	1.19 ± 0.26
SANAE	22	0.62 ± 0.12
Waterfront		
Gough	20	0.17 ± 0.04
Marion	42	0.18 ± 0.03
SANAE	21	0.18 ± 0.05

Decker V2405) fitted with a nylon mesh filter to recover any remaining seeds. To obtain a measure of drop-off when cargo was being moved around within Antarctica, 12 cargo units, which had not previously been used in the experiment, were seeded using the same specifications as when seeding cargo for the initial stage of the journey. These seeds were recovered at the end of the season, approximately one month later.

As part of the SANAP policy to reduce non-indigenous introductions to the Antarctic region, prior to arriving at any SANAP station all passengers are subject to a "boot washing" procedure in which clothing and equipment are checked for propagules (de Villiers et al. 2006). From pilot studies we know that this procedure is close to 100% effective because it involves visual inspection of washed footwear. Our aim was to investigate drop-off in the absence of this procedure, given that it is not uniformly practiced across those visiting the Antarctic. Thus, immediately after the boot-washing procedure, marked, sterilized seeds (30 seeds per item, 10 of each size class) were placed in the field clothing of 12 passengers (eight station-based personnel and four field-based personnel). Items included in the experiment were: outer jacket, outer trousers, hat, gloves, socks, boots, and rucksacks. Approximately one month later, at the end of the field season, any remaining seeds were recovered using the standard passenger luggage survey methodology.

A logistic regression assuming a binomial distribution and a logit-link function was implemented in R version 2.3.1 (R Development Core Team 2008) to compare the percentage of seeds that dropped off from cargo using seed species and voyage stage as categorical predictors. A second model was constructed to compare the percentage of drop-off in passenger luggage using clothing item, seed species, and station-based or field-based designation as categorical predictors.

Effect of washing on germinability

To test the effect of washing treatments on germinability, four species from genera commonly found entrained in passenger luggage were selected: *Avena sativa*, *Lolium perenne*, *Poa trivialis*, and *Agrostis stolonifera*. Seeds were treated under conditions representative of those that would be available to expeditioners using a home washing machine. These were: no detergent (distilled water), biological washing powder (Skip Intelligent, Unilever, South Africa), and a non-detergent-based soap designed for washing outdoor clothing (Tech Wash, Nikwax, UK). Batches of 100 randomly selected seeds from a commercial seed mix of the relevant species (Advanced Seed, Krugersdorp, South Africa) were each added to 50 mL of each of the treatment solutions and held at test temperatures of 20°, 30°, 40°, 50°, and 60°C for one hour using a Grant LTD6 water bath (Grant Instruments, Cambridge, UK). Thereafter, excess water was removed and seeds were placed in batches of 25 on nutrient agar (Merck Biolab Bacteriological agar, Wadevile, Gauteng, South Africa) and placed in an incubator at 21°C on a 12:12 (light : dark) cycle. Seeds were checked daily for the emergence of the radicle for up to eight days, after which time fungal contamination halted the experiment.

Performance curves of temperature against number of days until germination were constructed for each species and each treatment. Logit regressions using a quasi-Newton function (Statistica, version 8; StatSoft, Tulsa, Oklahoma, USA) were used to determine the temperature at which 50% mortality is reached (LT50). The influence of temperature and washing treatment on germination was analyzed using a generalized linear model in R version 2.3.1 (R Development Core Team 2008) assuming a binomial error distribution and using a logit-link function.

RESULTS

Initial examination revealed that samples often contained fragments of invertebrates, organic material, and plant parts and seeds. Although the organic material likely contained microorganisms, and some plant fragments may have been capable of vegetative growth, these could not be identified and were excluded. The most abundant propagule type was seeds. While it is accepted that not all of the seeds collected would be viable, analyses have focused on these as an easily quantifiable and identifiable propagule. This is a reasonable first step, given the significance of vascular plants as invasives in the region (Frenot et al. 2005).

Local propagule pool and entrainment in cargo

In total, 193 units of cargo were surveyed and 800 seeds collected (Table 1) with representatives from 22 families and 57 genera (see Appendix C for the list of taxa found). The majority of samples contained very few seeds, although some items contained as many as 47 (see Appendix A).

Using the Chao 2 estimator, rarefaction curves for both family- and genus-level richness were constructed for each voyage, and all appeared to reached their asymptote, indicating that sampling was sufficient to

TABLE 2. One-way analyses of similarity (ANOSIM) global test R values for taxonomic similarity in different classes of cargo.

Class	Family	Genus
Packing location	0.017	0.05*
Voyage destination	0.072**	0.037*

* $P < 0.05$; ** $P < 0.001$.

detect the majority of taxonomic groups (see Appendix D for rarefaction curves) and therefore allowed analyses of taxonomic similarity to be conducted. Small differences in taxonomic composition at the family and genus levels were found in samples destined for each of the research stations, and differences were also found between samples collected from cargo packed at the Waterfront and Paarden Eiland at the genus level (Table 2). However, the effect size is small and in all cases the R value was close to zero, and so, although differences are statistically significant, they are not biologically meaningful.

The vegetation surveys revealed that 56 species of vascular plant were present within a 500 m radius of the Paarden Eiland Stores and 13 species within 500 m of the Waterfront stores (see Appendix E for list of species found). Twenty-four of these species are known to be established aliens in the Antarctic region and a further 12 have congenerics that are known to be established aliens (Frenot et al. 2005; J. D. Shaw and S. L. Chown, *unpublished data*). For cargo packed at Paarden Eiland, 77% of families and 78% of genera found in the local vegetation were found in the cargo. For cargo packed at the Waterfront, 75% of families and 85% of genera found in the local vegetation were found in the cargo.

Of the propagules that were entrained within cargo, 70% of the families and 64% of the genera were from taxa that are known to be established aliens in the Antarctic region. When only Marion Island cargo and aliens are included, 20% of families and 16% of genera found in the cargo are established aliens on the island. For cargo traveling to Gough Island, 36% of families and 17% of genera found in cargo are established aliens on the island.

When considering what proportion of established alien species in the Antarctic region are found in samples, when all known aliens are included, 22% of alien families and 18% of alien genera are represented. However, when Marion Island is considered separately, 66% of families and 53% of genera that are known aliens on the island were found among cargo samples, and for Gough Island, 55% of alien families and 29% of alien genera were found among samples.

Entrainment in passenger luggage

Over the two-year sampling period, 606 seeds were collected from 933 items of clothing originating from 127 passengers (Table 3). Data were strongly right-skewed, with the majority of items surveyed containing no seeds, although four samples harbored more than 20 seeds (see Appendix A). Twenty families and 70 genera were represented.

Rarefaction curves for both family- and genus-level richness were constructed for each voyage using the Chao 2 estimator, and all appeared to reach their asymptote, indicating that sampling was sufficient to detect the majority of taxonomic groups (see Appendix F for rarefaction curves). For all categories of passenger luggage, the R values were close to zero, indicating that taxonomic composition of propagules found in samples was similar (Table 4). Significant differences in taxonomic composition of propagules were found between items but the effect size is extremely small and therefore not considered biologically meaningful.

Of the propagules that were entrained within passenger luggage, 80% of the families and 64% of the genera were from taxa that are known to be established aliens in the Antarctic. When only propagules collected from passengers traveling to Marion Island were considered, 30% of families and 17% of genera found in luggage are established aliens on the island. For Gough Island, 50% of families and 25% of genera found in luggage are established aliens on the island.

When considering what proportion of alien species already established in the Antarctic region were found in samples, 25% of alien families and 22% of alien genera were represented. For Marion Island, 100% of families and 71% of genera that are known aliens on the island were found among passenger luggage samples. For Gough Island, which has a much more diverse alien flora, the representation is much less, with 33% of alien families and 18% of alien genera found among samples.

Questionnaire data revealed that among all expeditioners, 28 countries had been visited in the 12 months prior to participating in the survey (Fig. 1). Most of the countries visited by expeditioners are at mid to high latitudes with a temperate or cold-temperate climate,

TABLE 3. Number of seeds (mean ± SE) found in passenger luggage sampled on voyages to Gough and Marion Islands and to the South African National Antarctic Expedition IV base (SANAE).

Destination	No. items sampled	Seeds/item	No. expeditioners sampled	No. seeds/expeditioner
Gough	64	0.69 ± 0.24	12	4.4 ± 1.80
Marion	451	0.95 ± 0.14	58	7.13 ± 1.25
SANAE	418	0.36 ± 0.05	57	2.67 ± 0.43

TABLE 4. One-way analyses of similarity (ANOSIM) global test R values for taxonomic similarity in different classes of passenger luggage.

Class	Family	Genus
Voyage destination	0.015	0.003
Item	0.041*	0.043**
Presence of Velcro	0.02	0.04
Issue	0.009	0.009

* $P < 0.05$; ** $P < 0.001$.

and so at the very coarsest scale are climatically similar to the island stations visited by SANAP. Furthermore, many of established Antarctic aliens originate in several of these areas (Frenot et al. 2005). A high proportion of expeditioners surveyed had recently traveled in the Antarctic (47%).

Comparison of composition of propagules in passenger luggage and in cargo

Many taxa were found in both cargo and passenger luggage samples, although a greater number of families and genera were found in passenger luggage. Small statistical differences in taxonomic composition of seeds found in cargo and passenger luggage were found at the family (ANOSIM global test $R = 0.22$, $P < 0.001$) and the genus (ANOSIM global test $R = 0.117$, $P < 0.001$) levels. However, although statistically significant, because of the low R values the differences are not considered meaningful.

Drop-off

Seed size had no effect on the proportion of seeds that dropped off from cargo ($\chi^2 = 2.41$, df = 2, $P = 0.503$) or clothing ($\chi^2 = 1.64$, df = 2, $P = 0.64$) after a month of activity. For cargo, drop-off was 20.3% ± 0.18% (mean ± SD). Voyage stage had no significant effect on the drop-off ($\chi^2 = 0.87$, df = 1, $P = 0.675$). For clothing, drop-off was 53.6% ± 28.8%. Drop-off did not differ significantly between clothing items ($\chi^2 = 7.49$, df = 7, $P = 0.588$) or between personnel who were field based vs. personnel who were station based ($\chi^2 = 7.49$, df = 2, $P = 0.882$). When only bags, trousers, and jackets were considered, items that contained Velcro had a lower drop-off than items that did not contain Velcro ($\chi^2 = 5.085$, df = 1, $P = 0.0241$; Fig. 2).

Mitigation

For cargo, packing location had a significant effect on propagule load, with cargo from the Paarden Eiland stores having a greater seed load than that from the Waterfront stores ($\chi^2 = 30.91$, df = 1, $P < 0.001$; Fig. 3a). This is perhaps unsurprising, given the greater abundance and diversity of propagules in the local source pool at Paarden Eiland, and gives a clear indication that an effective way to reduce entrainment is to reduce the abundance of local propagule sources. Voyage destination had no effect on propagule load ($\chi^2 = 3.79$, df = 2, $P = 0.1502$; Fig. 3b).

For clothing, generalized linear models indicated that some categories of clothing harbored substantially more seeds than others, and therefore it is these items that cleaning processes or management action should target. Number of seeds per item varied significantly with destination ($\chi^2 = 22.04$, df = 2, $P < 0.001$; Fig. 4a), with items surveyed on the way to Marion and Gough Islands having substantially higher seed loads than those surveyed on the way to SANAE. Number of entrained

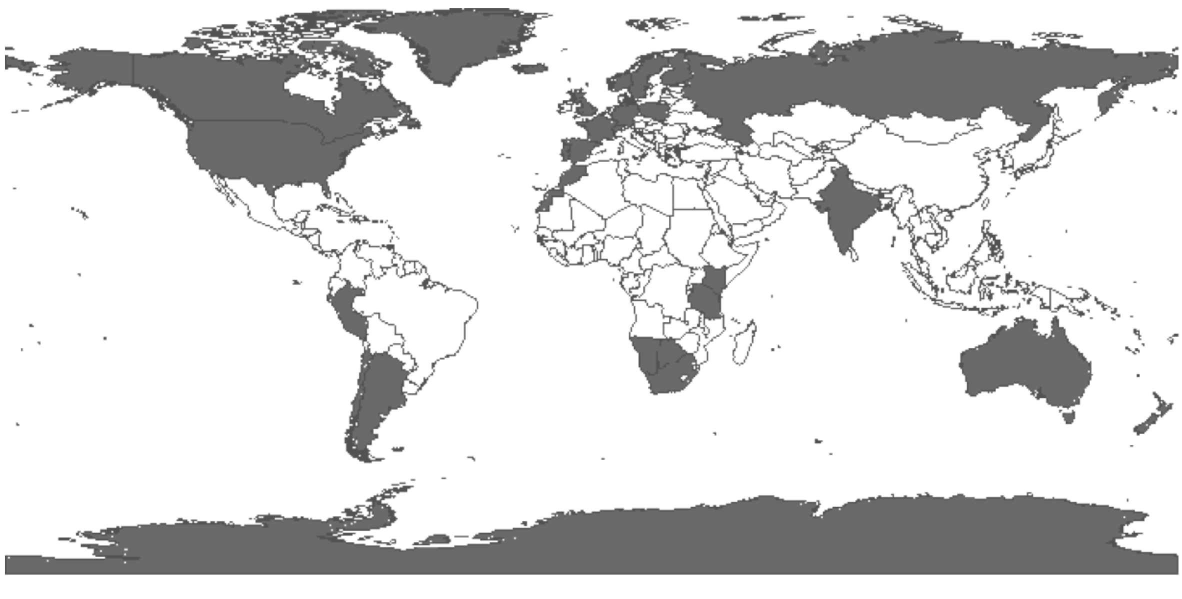

FIG. 1. Countries and regions visited by expeditioners (gray areas) in the 12 months prior to participating in a passenger luggage survey that quantified the initial dispersal of alien species into the Antarctic region associated with the South African National Antarctic Programme (SANAP).

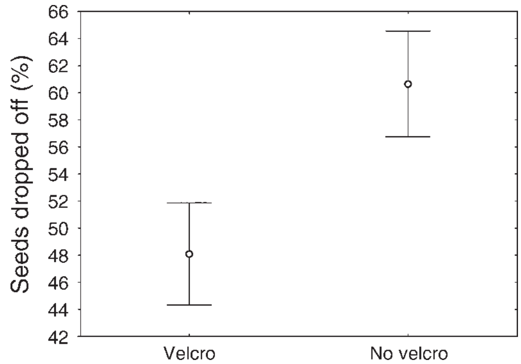

FIG. 2. Percentage of seeds (mean ± SE) that dropped off clothing items with and without Velcro, after the detection correction factor had been applied (see *Methods: Propagule drop-off* for details).

seeds also varied significantly with item ($\chi^2 = 76.01$, df = 7, $P < 0.001$; Fig. 4b), with socks and bags having the greatest seed loads. Passengers' own clothing harbored greater numbers of seeds than clothing that was issued by SANAP ($\chi^2 = 42.52$, df = 1, $P < 0.001$; Fig. 4c). Presence of Velcro was not significant when included in the main model ($\chi^2 = 1.64$, df = 1, $P = 0.2003$), but when only items that commonly had Velcro (waterproof trousers and waterproof jackets) were included in analyses, those with Velcro harbored a greater number of seeds than those without it ($\chi^2 = 4.90$, df = 1, $P = 0.0268$; Fig. 4d).

The most commonly employed cleaning technique, and the one which is most readily available to expeditioners, is washing in a commercial washing machine. For all species, washing temperature had a significant effect on germinability, but no significant effect of washing treatment was found, except for *Avena sativa*, which had low germinability when exposed to biological washing powder (Table 5). High levels of germinability were retained when seeds were exposed to washing temperatures commonly used to clean outdoor clothing (i.e., 40°C). Germinability did not start to decline until seeds were exposed to temperatures in excess of 50°C, and seeds were not sterilized until they had been exposed to temperatures of 70°C (Fig. 5). Although standard washing machines are capable of operating in excess of this temperature, and so are, at least in theory, capable of sterilizing seeds, washing garments made of specialist fabrics at high temperatures can affect their durability and performance (Grimshaw 2005). Temperature at which 50% of the population fail to germinate ranged between 39°C and 53°C (Table 5). Many specialist fabrics can be safely washed at these temperatures, indicating that although washing does not sterilize seeds, it may have some effect on the germination ability.

DISCUSSION

Patterns and their implications

Owing to the ban on the introduction of plants and animals to the Antarctic and many of its surrounding islands (de Villiers et al. 2006, Mansfield and Gilbert 2008), the major introduction pathway to the region is a vector-based, stowaway one (see Hulme et al. 2008). Only for islands with permanent human settlements (such as Tristan da Cunha and the Falkland Islands) are other pathways likely to be involved. Nonetheless, even within the single pathway that is significant for most of the region, much variation exists in the numbers (and to a more limited extent the identities) of propagules associated with different source areas and items. This variation suggests that several options are open to reduce the extent of propagule transfer, as is required by national and international legislation across the region, by relatively straightforward, and in many cases cost-effective, interventions.

In terms of taxon identity, the cargo and passenger luggage surveys revealed that seeds from similar genera and families were being entrained by both pathways and that variation among items within each category was low. Given the diverse travel histories of expeditioners

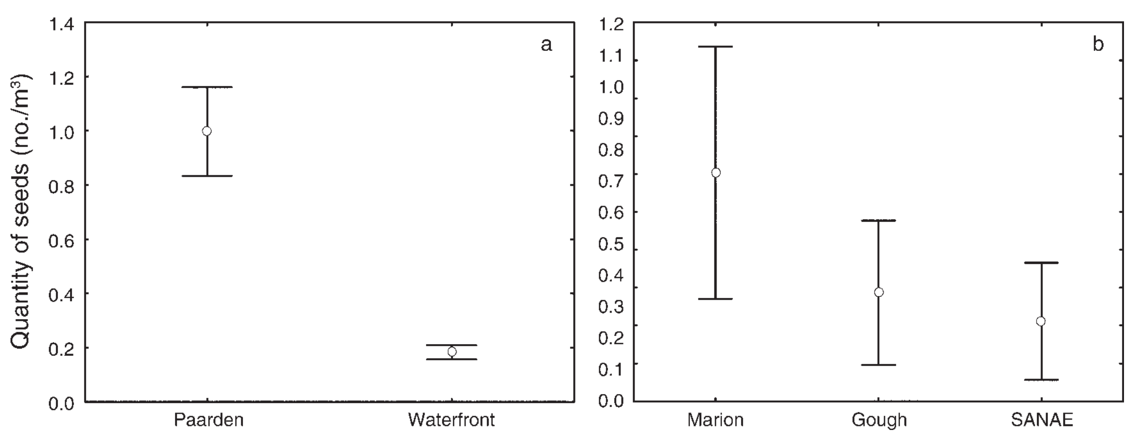

FIG. 3. Quantity of seeds (mean ± SE) found in (a) cargo items packed at Paarden Eiland and the Waterfront stores and (b) cargo items destined for Marion Island, Gough Island, and to the South African National Antarctic Expedition IV base (SANAE).

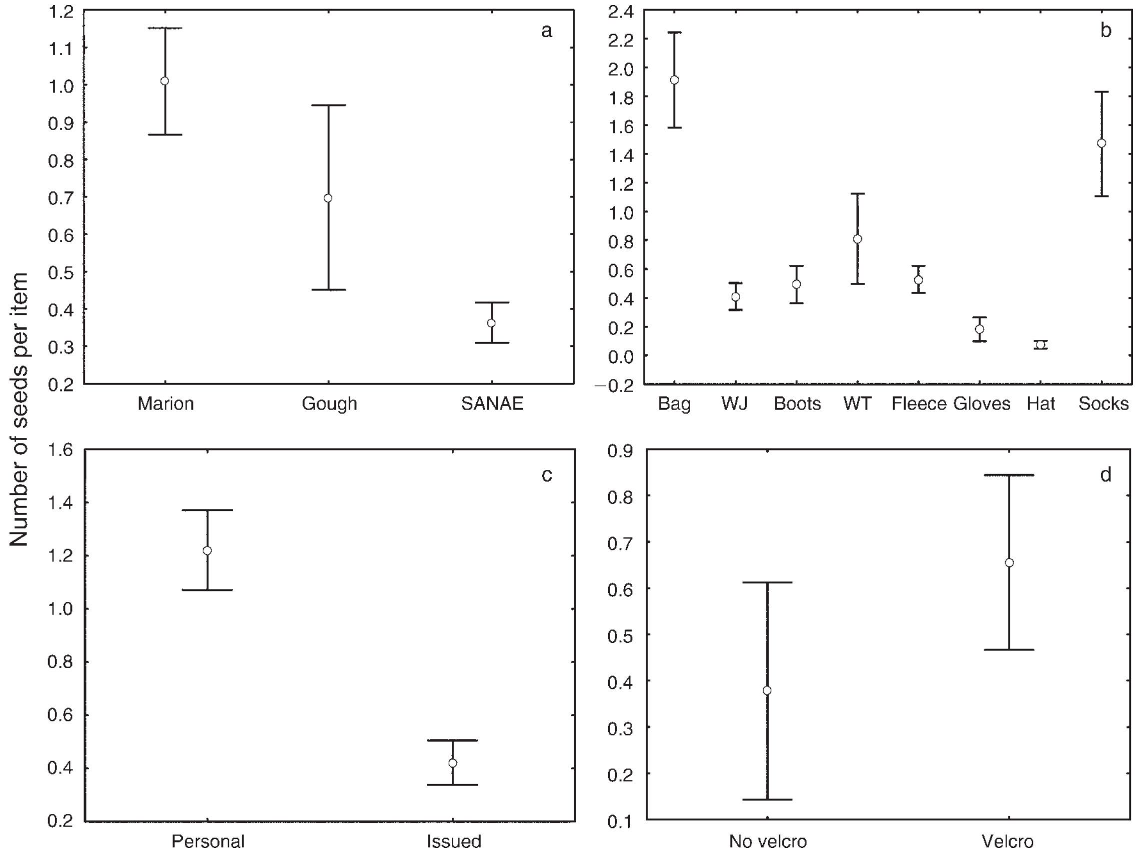

FIG. 4. Number of seeds found per item (mean ± SE) in each category of passenger luggage by: (a) destination (Marion Island, Gough Island, and to the South African National Antarctic Expedition IV base [SANAE]); (b) personal item type; (c) personal origin vs. issued by the South African National Antarctic Programme (SANAP); (d) presence of Velcro on the item. For (b), abbreviations are: WJ, waterproof jacket; WT, waterproof trousers.

and therefore large potential pool of species that had the potential to become entrained and the different exposure histories of cargo and luggage, this suggests that a relatively small pool of weedy species is being entrained by both methods, and the majority of taxa found in samples had no specific adaptations to become entrained by dispersal vectors (Liu et al. 2008). Thus, encounter frequency, such as with commonly entrained groups with high reproductive outputs (e.g., Asteraceae and Poaceae; Pyšek and Richardson 2007) is likely to be the major method of entrainment. Indeed, the distribution of propagule number among the various taxonomic groups suggests that this is the case, with the proportions of propagules in the various taxonomic groups reflecting not only those families known to contain the highest numbers of invasives worldwide (Pyšek 1998), but also reflecting, to a large extent, the distribution among genera and families of the species known to have

TABLE 5. Generalized linear model results for the effects of temperature and treatment on germination in four Poaceae species and the LT50 under each washing treatment.

	χ^2		LT50 (°C)		
Species	Temperature (df = 6)	Treatment (df = 2)	Distilled water	Tech Wash	BWP
Avena sativa	53.33**	71.71*	47.6 ± 0.31	39.5 ± 0.525	···
Lolium perenne	57.20**	62.46	53.0 ± 0.35	52.0 ± 0.35	49.3 ± 0.35
Poa trivialis	65.24**	64.91	50.7 ± 0.86	50.3 ± 0.14	48.1 ± 0.965
Agrostis stolonifera	61.50**	62.23	50.4 ± 0.43	49.2 ± 0.55	47.5 ± 0.73

Notes: *Avena sativa* never achieved 50% germination success under a biological washing powder treatment, and therefore it was not possible to calculate LT50. Abbreviations are: LT50, the temperature at which 50% mortality is reached; Tech Wash, a non-detergent-based soap designed for washing outdoor clothing; BWP, biological washing powder.

* $P < 0.05$; ** $P < 0.001$.

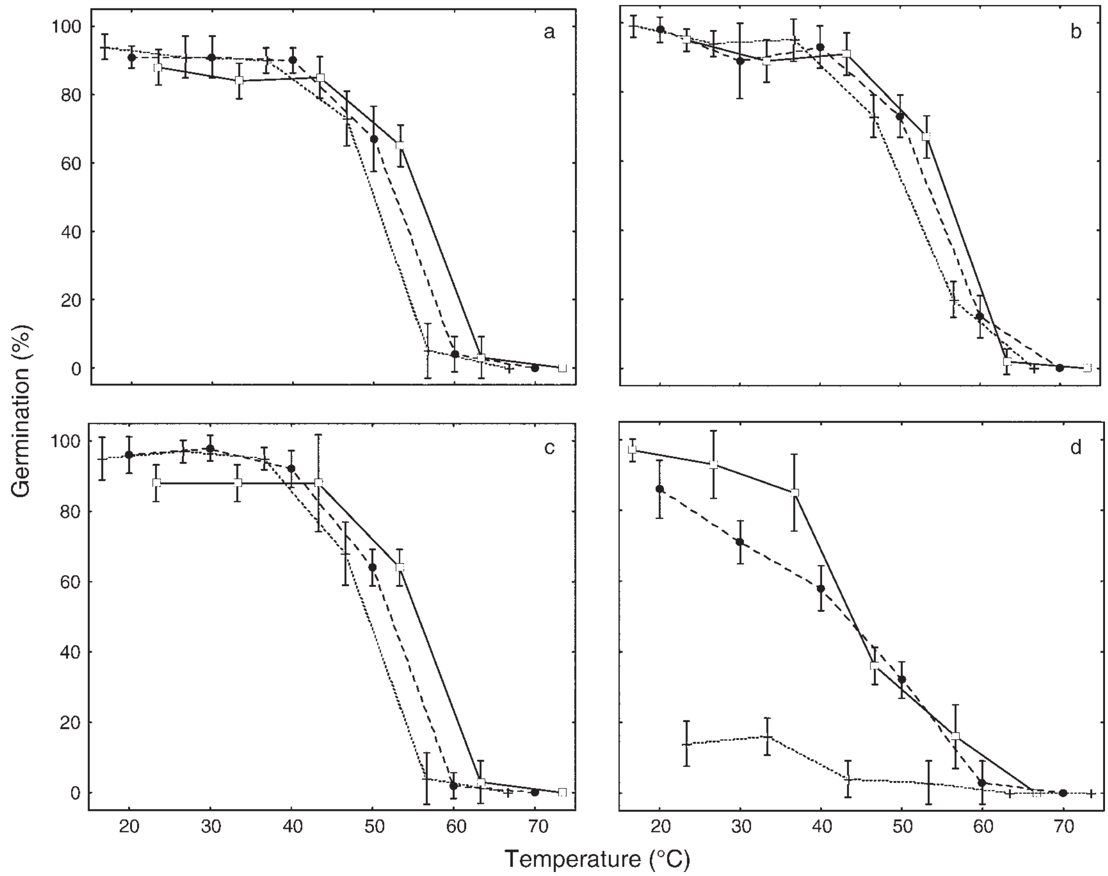

FIG. 5. Effect of temperature on germination (mean ± SE) of (a) *Agrostis stolonifera*, (b) *Lolium perenne*, (c) *Poa trivialis*, and (d) *Avena sativa* after washing with distilled water (open squares), Tech Wash (a non-detergent-based soap designed for washing outdoor clothing; solid circles), and a biological washing powder (crosses).

been introduced to the Antarctic region (Frenot et al. 2005). For example, all of the families and 70% of genera that are known aliens on Marion Island were found in passenger luggage samples. By contrast, for Gough Island, the current propagule input represents much less of the established alien flora on the island, which indicates that some aliens were introduced via pathways that are now obsolete. For example, two alien genera (*Solanum* and *Verbena*) were not found in any of the samples collected. In the case of *Solanum tuberosum* this is because the species was introduced intentionally and has now escaped human control (Jones et al. 2003) and so represents a different invasion pathway (i.e., escape; Hulme et al. 2008). However, it is thought that *Verbena bobariensis* was introduced unintentionally (Ryan 2007), probably during station construction, and so should probably be considered a different pathway to ordinary relief voyages because construction materials are known to harbor greater than and often different propagule loads from the usual cargo (Bergstrom and Smith 1990).

The relatively high similarity of the propagule load across the cargo and luggage suggests either that entrainment is highly local or is occurring in highly disturbed areas that often have similar suites of weedy species (Prinzing et al. 2002). The fact that the propagule identity of the less-invaded Waterfront cargo site is entirely nested within that of the Paarden Eiland site is indicative of the fact that entrainment from highly disturbed areas is important, because these sites are located several kilometers apart. Likewise, that the luggage and cargo surveys have similar propagule identities suggests that these items, coming from distant sites, carry similar suites of species. In consequence, the present data support the idea that transport hubs provide ideal stepping stones for invasive species as these facilities are commonly in semi-industrial locations, close to areas of disturbed ground, and are likely to receive high numbers of alien species from across the globe (Pauchard and Alaback 2004, Blumenthal 2006, Hierro et al. 2006). Indeed, it seems likely that the SANAP logistics operation forms a small component of a much larger, global, self-perpetuating cycle whereby weedy species proliferate in disturbed areas, in consequence have an elevated chance of becoming entrained in cargo and transported to other, similarly disturbed habitats, and in turn act as a source population to facilitate invasion to other locations (Greenberg et al.

PLATE 1. A variety of alien species have successfully colonized the Antarctic region. One such example is the introduced grass *Agrostis stolonifera*, which is shown here dominating the vegetation surrounding the Van der Boogaard River on sub-Antarctic Marion Island. Photo credit: Justine Shaw.

1997, Alston and Richardson 2006). This has important implications for biosecurity policy for the Antarctic because nearly all Antarctic shipping operations use commercial ports and because substantial volumes of cargo are moved through interconnected transport networks (Drake and Lodge 2004).

Besides transporting a substantial diversity of propagules, logistics operations also transfer substantial numbers of propagules. Expeditioners on the SANAP program carry, on average, between 2.67 (SANAE) and 7.13 (Marion Island) seeds per person (Table 3). This variation in propagule pressure between destinations is likely to be a result of varying disciplines of the scientists, with mainly field-based biologists visiting Marion and station-based atmospheric scientists visiting SANAE. In addition, field clothing worn at SANAE, which is suited for very-low-temperature field conditions, is unlikely to be worn elsewhere, and therefore there are very limited opportunities for propagule entrainment. At present, the only other nation that has attempted to quantify the propagule pressure associated with a national Antarctic program is Australia (Whinam et al. 2005). Here it was found that on average passengers were each carrying ~15 seeds, substantially more than the values calculated for South African expeditioners. The difference in propagule load could be attributed to the operational procedure of the respective Antarctic programs, with South African expeditioners often using their clothing for the first time only once they arrive in the Antarctic, whereas at the time the Whinam et al. (2005) study was conducted, Australian expeditioners routinely used their equipment for field training in the Tasmanian alpine regions prior to departure (Chown 2003), where substantial propagule entrainment could have occurred. Nonetheless, it is clear that expeditioners' luggage and cargo act as vectors for a variety of alien and often-invasive species that either have established in the region or could do so.

Most logistics operations center around a research station, where all cargo and expeditioners are initially offloaded and where the majority of alien species first become established (Bergstrom and Smith 1990). However, modern logistics operations are facilitating rapid discharge to the field (via fixed-wing aircraft in Antarctica and helicopters in Antarctica and on the surrounding islands). In consequence, logistics operations could facilitate the rapid range expansion and jump dispersal of newly established aliens (Bergstrom and Smith 1990, Gremmen and Smith 1999). Moreover, the presence of endemics such as *Acaena magellanica* in samples indicates that expeditioners also transport native species. Some native invertebrate species are known to have complex genetic structure (Frati et al. 2001, Mortimer and Jansen van Vuuren 2007, Myburgh et al. 2007), and there are indications that vascular plant populations may display a similar pattern (Mortimer et al. 2008). Transportation of species between populations could homogenize population genetic structure (Olden et al. 2004), with significant impacts not only on modern understanding of evolutionary dynamics in the region (Myburgh et al. 2007), but also on the evolution of the species (Frati et al. 2001, Stevens and Hogg 2003) and their ability to withstand the rapid environmental change characteristic of many islands and the Antarctic Peninsula (Convey 2006). Moreover, at least in Antarctica, where long-distance flights between field sites are becoming more common, the risks for the movement of species to sites where they have not occurred previously might also be higher than is perhaps currently acknowledged. Although vascular plants are of little concern in continental Antarctica, the principles apply as much, or perhaps more so, to species such as invertebrates, mosses, and algae.

Mitigation

Although many national operators, including SANAP, have stringent management procedures in place (de Villiers et al. 2006, Davies et al. 2007), it is clear that large numbers of propagules are still being transported into the Antarctic region (Cooper et al. 2003, Whinam et al. 2005, Hughes et al. 2006, Lewis et al. 2006). Therefore, if the flow of alien species into the region is to be halted, an urgent need exists to develop improved mitigation measures. Management action should be targeted at cargo and passenger items that contain high numbers of propagules and have high propagule deposition rates.

For cargo, entrainment and drop-off is greatest when the cargo is being intensively handled, such as at warehouses and during loading and off-loading areas. To minimize the numbers of propagules that are entrained in cargo, it should be loaded in an area free from weedy plants. Equally, because drop-off is also highest in these areas, careful monitoring and immediate removal of any newly established species will help prevent the spread of aliens. This has been shown to be successful on Macquarie Island, where two introduced plants (*Anthoxanthum odoratum* and *Rumex crispus*) with highly localized distributions were removed and have not since recolonized (Copson and Whinam 2001). Cargo containers can also be designed to minimize seed entrainment (Whinam et al. 2005) and can be inspected and cleaned thoroughly prior to loading and to transfer to a cargo hold. Such measures typically do not require large infrastructure and personnel investments, and, where expensive containers are to be replaced, they can be phased in as older items age or are damaged. Greater expense may be encountered if warehouses are situated close to vacant, weed-infested land and a change to a new warehousing area or the development of an appropriate spraying program is required. However, these costs are likely to be low relative to the costs of eradication efforts (Gremmen et al. 2001, Bester et al. 2002).

In the case of expeditioner luggage, it is clear that items such as bags and socks have high propagule loads and that personal gear poses a higher risk than items that are issued by the logistics operator (which has all items thoroughly cleaned between field trips). Simple but effective measures, such as the use of new socks for all expeditions and the thorough cleaning of bags will clearly substantially reduce propagule load. After Whinam et al. (2005) highlighted the risk of Velcro as a biosecurity risk, the Scientific Committee on Antarctic Research countries discouraged the use of clothing with Velcro (Hull and Bergstrom 2006). Here we confirm Whinam et al.'s (2005) finding, but when the effects of entrainment and drop-off are disentangled, we find that although Velcro may harbor substantial propagule loads, these propagules are less likely to be expelled into the environment than propagules on Velcro-free items. Therefore, simply eliminating Velcro from field clothing is an ineffective way to reduce the risk of invasion. Rather, propagule entrainment in general must be minimized.

The washing of clothing is one of the most commonly applied procedures to prevent the transport of nonindigenous species in clothing (Chown et al. 2006, de Villiers et al. 2006, de Villiers and Cooper 2008). However, a clear conflict of interest exists between performance of clothing and the chance of alien introduction. Washing procedures had varying success, from being relatively effective (e.g., high-temperature treatments or biological washing powder on species such as *Avena sativa*) to having almost no effect (e.g., low-temperature treatments and Tech Wash). Although standard washing procedures are likely to reduce the number of viable propagules, some will survive, and because small founder populations have occasionally led to invasions (Gaston et al. 2003, Scott and Kirkpatrick 2005, Lee et al. 2007), simply reducing propagule pressure is not sufficient. If invasions are to be halted entirely, propagule pressure needs to be reduced to as close to zero as feasible. However, washing protocols that would sterilize seeds, such as high-temperature treatments, would also damage many commonly used fabrics (Grimshaw 2005), leading to a dramatic reduction in their performance. Possible alternatives include irradiation (Luckman 2000) or exposure to extremely low temperatures (Sharp and Hallman 1994). However implementation of such protocols would need a substantial policy revision and investment in infrastructure.

An alternative to inspection and washing is to ship new clothing to the research station of interest and to leave it there once it has been used initially (either for the return of long-term visitors or for reissue to new expeditioners). This practice is currently being implemented by the Australian Antarctic Division for high-risk items such as gaiters (D. Bergstrom, *personal communication*). Although this would not prevent intra-island (sub-Antarctic) or intra-area (Antarctic continent) movement of propagules, it would prevent the introduction of exogenous species. Research stations would need to be equipped with the means to clean and maintain equipment, but no substantial new infrastructure would be required. This therefore may be the most economically and ecologically sensible way to reduce the flow of alien species into the region with expeditioner clothing.

Biosecurity implications

The current work has demonstrated that substantial propagule pressure is associated with current scientific operations to the Antarctic, but that relatively straightforward measures are available to reduce this pressure. Most significantly, a change in the inspection and issuing procedures for expeditioner luggage and relatively inexpensive changes in cargo operations are likely to result in substantially reduced propagule loads. These procedures, at least in terms of expeditioners, apply as much to the tourist industry as they do to science logistics. However, they may be much more difficult to apply to large station construction operations, as are currently taking place across the region, and a different approach may be required. Moreover, the problem of propagule exchange within islands or between areas in Antarctica is yet to be adequately resolved.

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APPENDIX A

Frequency distribution of number of seeds found in cargo and expeditioner clothing (*Ecological Archives* A019-081-A1).

APPENDIX B

Percentages of seeds that were missed due to sampling error and that were used to calculate the correction factors that were used to offset for sampling inaccuracy in the clothing and cargo drop-off experiment (*Ecological Archives* A019-081-A2).

APPENDIX C

Percentage of total number of seeds collected represented by each of the families and genera found in cargo and passenger luggage samples (*Ecological Archives* A019-081-A3).

APPENDIX D

Sample-based rarefaction curves showing the increase in numbers of family and genera with increasing number of cargo units sampled for each voyage (*Ecological Archives* A019-081-A4).

APPENDIX E

Species of vascular plants growing within 500 m of the cargo packing locations at Paarden Eiland and the Waterfront and whether they are listed on the Global Invasive Species Database (*Ecological Archives* A019-081-A5).

APPENDIX F

Sample-based rarefaction curves showing the increase in numbers of family and genera with increasing number of passenger luggage items sampled for each voyage (*Ecological Archives* A019-081-A6).